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Temperature-Dependent Physiology of *Poa secunda*, a Cool Season Grass Native to the Great Basin, United States[1]

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Abstract—*Poa secunda* Presl. is one of the few native perennial bunchgrasses in the Intermountain West to persist and co-occur with the invasive annual *Bromus tectorum* L. following widespread overgrazing and frequent wildfires. To identify potential mechanisms responsible for the co-occurrence of *P. secunda* with *B. tectorum*, respiration rates (R_{CO_2}) of eight populations were measured at 10, 20, and 30°C on laboratory-grown plants by infrared gas analysis. In addition, R_{CO_2} and metabolic heat rates (q) of nine field-grown populations were measured at 10 and 20°C using calorimetry on eight dates over a growing season to compare temperature-dependent physiology of *P. secunda* with previous published patterns for *B. tectorum.* Laboratory respiration rates of *P. secunda* populations suggest considerable intraspecific variation in physiological response to temperature. Changes in slope for R_{CO_2} and q over the growing season were steeper at 20 than at 10°C, suggesting that *P. secunda* populations are more capable of maintaining steady rates of metabolism at low than at high temperatures. However, growth rates of *P. secunda* were relatively lower than those for *B. tectorum* at 10°C. Calculations of growth rates and efficiency of converting substrate carbon into biomass of *P. secunda* consistently remained positive, while those for *B. tectorum* rapidly declined at temperatures above 10°C. These data suggest that *P. secunda* co-occurrence with *B. tectorum* over a broad range of plant communities in the Intermountain West may be partially explained by having a similar ability to maintain positive and stable growth rate at low temperature. In addition, the greater ability of *P. secunda* to maintain growth rates and metabolic efficiency at higher temperatures than *B. tectorum* may allow this perennial grass to compensate for the greater relative growth rates of *B. tectorum* at low temperature.

Key words: Poa secunda - Bromus tectorum - dark respiration - calorimetry - shrub steppe - metabolic heat - temperature

INTRODUCTION

Past range management practices in the Intermountain West and Great Basin of the United States have resulted in widespread loss of native perennial grasses [1] and replacement by the invasive annual grass, *Bromus tectorum* L., cheatgrass, or downy brome [2, 3]. *Poa secunda* Presl., Sandberg's bluegrass, is a native perennial grass known to have a similar phenology to *B. tectorum* [4]. In addition, *P. secunda* has been shown to be less damaged by fire than other native bunchgrasses in shrub–steppe communities of the Intermountain West [5]. *B. tectorum* and *P. secunda* are co-dominants in many of the drier portions of the Columbia Plateau and in much of the Intermountain West [6, 7].

Few studies have compared the physiological mechanisms responsible for similar phenology between *B. tectorum* and *P. secunda* [4, 8]. Overlap in growth periods and acquisition of limiting water and nutrients between these species suggests that their physiology may respond similarly to environmental factors such as temperature. However, methods capable of quantifying physiological responses integrated over the growth period are needed to determine potential mechanisms.

[1] The text was submitted by the authors in English.

Abbreviations: PPFD—photosynthetic photon flux density; q—metabolic heat rate; Q_{10}—respiratory quotient; R_{CO_2}—respiration rate.

Table 1. Origin of *P. secunda* populations used

Location	Elevation, m	Experiments	
		laboratory	field
Hell's Canyon, Idaho	ca 700		+
Payette, Idaho	ca 700		+
Kuna Butte, Idaho	ca 950	+	+
East Boise, Idaho	ca 950	+	
Boise Front, Idaho	ca 975	+	+
Orchard, Idaho	ca 960		+
Mayfield, Idaho	ca 1110	+	
Grasmere, Idaho	ca 1560	+	+
Rogerson, Idaho	ca 1650	+	+
Jackpot, Nevada	ca 1660	+	+
Three Greek Rd., Idaho	ca 1690	+	+

Metabolic calorimetry is one method that monitors physiological activity at different temperatures and across the growing season and provides important information about the physiology and phenology of plants. Both dark respiration rate (R_{CO_2}) and heat rate (q) can be measured by calorimetry. Values for R_{CO_2} and q can be used to calculate specific growth rate and substrate carbon conversion efficiency as a function of temperature [9–11].

Calorimetry was recently used to determine growth rates and efficiency of converting photosynthetic substrate to structural carbon as functions of temperature in different *B. tectorum* populations [12, 13]. Both experiments indicated that growth rates and carbon conversion efficiencies of *B. tectorum* populations rapidly declined within the temperature range of 10 to 20°C. Accordingly, in the study reported here, we seek to quantify the physiological activity of distinct *P. secunda* populations during a growing season using calorimetry and to contrast these responses with those of *B. tectorum.* We conducted an initial experiment with laboratory-grown *P. secunda* plants to evaluate the temperature dependence of R_{CO_2} within the temperature range of 10 to 30°C. In a second experiment, calorimetric measurements were made at 10 and 20°C on plant material collected from field-grown *P. secunda* from common gardens at two widely separated locations in the Intermountain West. Calorimetric data from the field experiment were used to calculate growth rate and substrate carbon conversion efficiency based on these metabolic measurements. We anticipated that the physiological and metabolic responses of *P. secunda* may provide insights into the mechanisms associated with its persistence and phenology similar to *B. tectorum.*

MATERIALS AND METHODS

Plants from 11 native populations of *P. secunda*, Sandberg's bluegrass, were each established in two common gardens in spring 1994 at Orchard, Ida. (43° 20′ N, 116° 1′ W) and Nephi, Ut. (39° 37′ N, 111° 51′ W). Orchard is at an elevation of 960 m with an average annual precipitation of 27 cm. Soils at Orchard are classified as xerollic haplargids, Lankbrush series located on lacustrine alluvium [14]. Elevation at Nephi is 1600 m with an average annual precipitation of 38 cm. Soils at Nephi are classified as calcic agrixerolls, Nephi series [15]. Plots containing 24 plants of each population were randomly planted in three locations at each garden. Here, we refer to the populations by local landmarks or establishments (Table 1).

Laboratory experiment. Seeds were collected from eight of the *P. secunda* populations located at the Nephi common garden (Table 1) and germinated at 20°C. Each population was established in three separate 1-l pots filled with an organic potting soil by planting 5 seedlings per pot. Plants were thinned to three evenly sized plants per pot after one month. Plants were grown in a laboratory growth chamber under supplemental white light (PPFD = 200 μmol/(m^2 s); 16-h photoperiod) at 20 to 23°C and watered every other day with a quarter-strength Hoagland solution. Plants were grown for seven months before respiration rates (R_{CO_2}) were measured by transferring randomly chosen pots into a dark chamber for 0.5 h to dark-adapt plants. During each measurement period, one pot from each population was measured within a 3-h period by continually placing new pots into the dark chamber 0.5 h before measuring the three plants. Approximately 100 mg of young expanding leaves located on the periphery of plants was excised and placed in a dark 7-cm^3 cuvette attached to an LI-6250 infrared gas analyzer (Li-Cor, United States). Temperature dependence of R_{CO_2} was obtained by submerging the sealed cuvette in a constant temperature bath for 5 min prior to measuring R_{CO_2} in the ordered sequence of 10, 20, and 30°C. This entire procedure was repeated two additional times within a 1-week period for the two remaining pots for each population. Each sample was oven-dried at 70°C for 24 h for dry matter determination. R_{CO_2} data are expressed as nmol CO_2/(g dry wt s). The factors by which R_{CO_2} increases with a 10°C change in temperature (Q_{10}, respiratory quotient) were calculated from these data for two temperature ranges: 10 to 20°C and 20 to 30°C. R_{CO_2} and Q_{10} data were analyzed with repeated measures ANOVA and two-way ANOVA, respectively. Tukey's HSD procedure was used to determine significant differences ($P < 0.05$) between populations [16].

Field calorimetry experiment. Young expanding leaves from nine *P. secunda* populations (Table 1) were collected from both common gardens over a 9-week

period on eight dates beginning on March 27 and ending on May 22 during spring 1996. Samples were kept cold in an ice chest until calorimetric measurements were taken within 18 h following collection. Approximately 100 mg of leaf tissue was cut into 1-cm segments and placed into calorimeter ampules. Ampules were placed in differential, heat conduction, temperature-scanning calorimeters (Model 7707, Hart Scientific, United States) operated in isothermal mode according to published procedures [11, 17]. Measurements of metabolic heat rates, q (mW/g), and R_{CO_2} (nmol CO_2/(g s)) were made at 10 and 20°C and expressed on a dry mass basis after samples were placed in a vacuum oven at 70°C for 24 h. Three samples (a composite of numerous plants) from each population were measured at each sampling date. This sampling procedure was designed to evaluate the physiological variability that exists within this species as opposed to making robust comparisons among populations. The slopes of q and R_{CO_2} over the growing season for *P. secunda* populations from the Nephi and Orchard gardens were compared using the mean square drop procedure [18].

Calculated responses. Values for q and R_{CO_2} were used to calculate specific growth rate and substrate carbon conversion efficiency according to the model proposed by Hansen *et al.* [9, 10]. This model describes specific growth rate (R_{SG}) (i.e., the anabolic rate of conversion of substrate carbon into structural biomass) with equations (1) and (2):

$$R_{SG} = [-q - R_{CO_2}(1 - \gamma_P/4)\Delta H_{O_2}]/\Delta H_B, \quad (1)$$

$$R_{SG} = R_{CO_2}[\varepsilon/(1 - \varepsilon)], \quad (2)$$

where q is specific metabolic heat rate, R_{CO_2} is specific respiration rate, γ_P is mean oxidation state of substrate carbon oxidized to CO_2, ΔH_{O_2} is a constant equal to -455 ± 15 kJ/mol, ΔH_B is the enthalpy change for conversion of substrate to structural biomass by anabolism, and ε is substrate carbon conversion efficiency. Equation (1) is derived from the enthalpy balance for catabolism and anabolism and Thornton's rule, and equation (2) is derived from the chemical equation for aerobic metabolism. Combining equations to eliminate R_{SG} gives equation (3):

$$q/R_{CO_2} = -(1 - \gamma_P/4)\Delta H_{O_2} - [\varepsilon/(1 - \varepsilon)]\Delta H_B. \quad (3)$$

In this study, γ_p was assumed equal to zero (i.e., substrate C is carbohydrate), and ΔH_B was assumed to be constant (and not measured) and was not separated from R_{SG} or the ε function, $[\varepsilon/(1 - \varepsilon)]$. Growth rate was thus expressed as $R_{SG}\Delta H_B$ in units of μW/mg dry wt and substrate carbon conversion efficiency as $[\varepsilon/(1 - \varepsilon)]\Delta H_B$ in units of kJ/mol new biomass formed by anabolic processes.

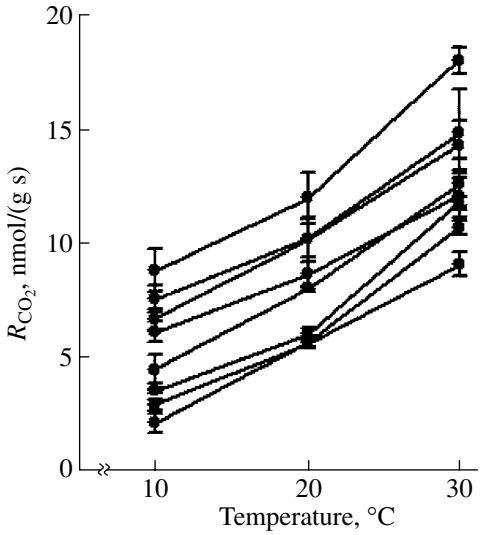

Fig. 1. Respiration rates (R_{CO_2}) of various *P. secunda* populations measured in the laboratory at three temperatures, represented by the means and their standard errors.

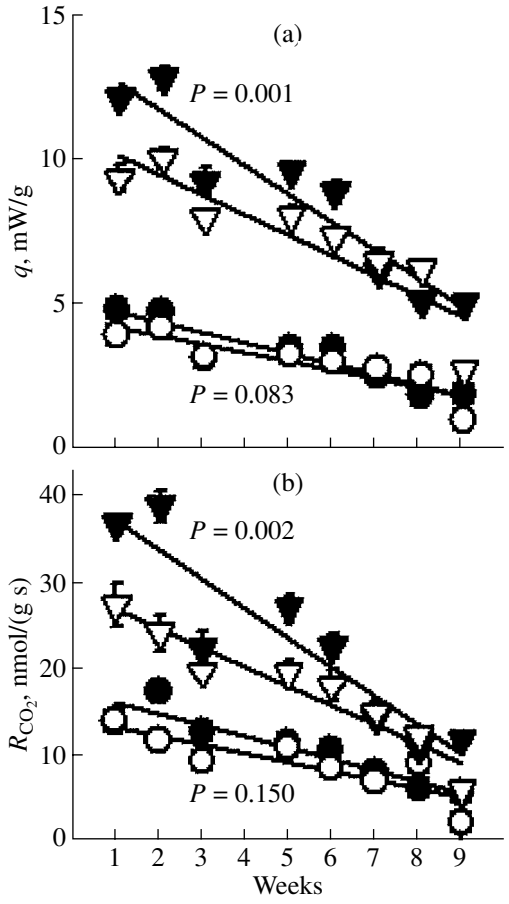

Fig. 2. (a) Metabolic heat rates (q) and respiration rates (R_{CO_2}) of *P. secunda* populations measured at 10 (circles) and 20°C (triangles) from plants grown in Orchard, Idaho (open symbols) and Nephi, Utah (closed symbols). P-values correspond to a comparison of regression lines for Orchard and Nephi populations at 10 and 20°C. Data are represented as the means ± standard errors.

Table 2. Respiratory quotient Q_{10}

Population	Q_{10} (10–20°C)	Q_{10} (20–30°C)
Kuna Butte	1.42 ± 0.12^{b}	1.40 ± 0.04^{b}
East Boise	1.70 ± 0.09^{b}	1.96 ± 0.06^{a}
Boise Front	1.36 ± 0.03^{b}	1.54 ± 0.16^{ab}
Mayfield	1.85 ± 0.24^{ab}	1.56 ± 0.12^{ab}
Grasmere	1.35 ± 0.05^{b}	1.43 ± 0.08^{b}
Rogerson	2.79 ± 0.47^{a}	1.87 ± 0.05^{a}
Jackpot	1.93 ± 0.20^{ab}	1.61 ± 0.08^{ab}
Three Greek Rd.	1.51 ± 0.06^{b}	1.41 ± 0.04^{b}

Note: The results are expressed as the means ± standard errors. Different letters indicate significant differences.

RESULTS

Laboratory experiment. Temperature and population had significant effects on R_{CO_2}, and the interaction of temperature with population was not significant, suggesting temperature had consistent effects across populations (Fig. 1). R_{CO_2} of Boise Front, Grasmere, and Three Creek Rd. populations (upper three lines) were significantly higher at all three temperatures than the East Boise, Jackpot, and Rogerson populations (lower three lines). Kuna Butte and Mayfield populations had R_{CO_2} values intermediate between these two groups. Respiratory quotients (Q_{10}) were significantly different between populations, but not between the temperature ranges of 10 to 20 and 20 to 30°C (Table 2). Rogerson had a significantly greater Q_{10} than all populations except East Boise.

Field calorimetry experiment. Metabolic heat rate (q) (Fig. 2a) and R_{CO_2} (Fig. 2b) of the *P. secunda* populations were greater at 20 than at 10°C over the 9-week evaluation. Rates were the highest in March at the beginning of the growing season and lowest in May as plants matured. Rates for q and R_{CO_2} measured at 20°C were twice as high as rates at 10°C on week 1. However, by week 9, the magnitude of difference between 10 and 20°C was at a minimum for q and was not significantly different for R_{CO_2} ($P > 0.05$). A statistical analysis of slopes revealed that q and R_{CO_2} responses at Nephi were significantly different than Orchard across the growing season only for 20°C.

Growth rate ($R_{SG}\Delta H_B$) and substrate carbon conversion efficiency ($[\varepsilon/(1-\varepsilon)]\Delta H_B$) as a function of temperature for weeks 1, 5, and 9 are shown in Fig. 3 to provide a general illustration of patterns of variation among the *P. secunda* populations. Growth rates were consistently low throughout the growing season and generally did not change between 10 and 20°C with the exception of two populations from Orchard on week 1. In addition, growth rates were generally more variable during early and mid-season (weeks 1 and 5) compared to late season (week 9), when rates were similar for

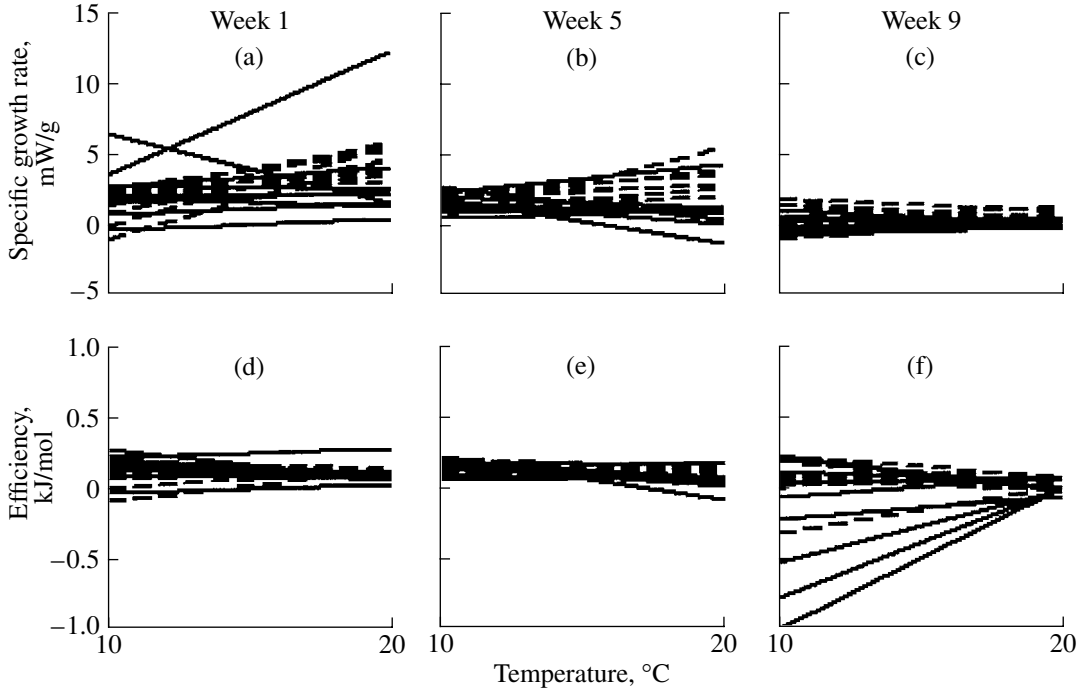

Fig. 3. (a–c) Specific growth rates ($R_{SG}\Delta H_B$) and (d–f) efficiency of converting photosynthetic substrate to structural carbon ($[\varepsilon/(1-\varepsilon)]\Delta H_B$) of *P. secunda* populations calculated for three dates in a growing season at 10 and 20°C. Solid lines indicate Orchard populations; dashed lines indicate Nephi populations.

populations at both Nephi and Orchard. The efficiency of converting substrate carbon into structural mass ($[\varepsilon/(1-\varepsilon)]\Delta H_B$) was consistently low but generally greater than zero in early and mid-season. In contrast, efficiencies were considerably more variable in late season, with numerous populations, primarily from the Orchard garden, displaying marked increases with temperature.

DISCUSSION

It has been suggested that the invasive annual grass *B. tectorum* remains dominant in shrub–steppe communities of the Great Basin, because few native perennial grasses exist to exploit the resource niche that was created following large-scale disturbance to native vegetation [12, 20]. Along these lines, we questioned if one of the native perennial grasses that shares a similar phenology with cheatgrass and that continues to persist with cheatgrass would have similar temperature-dependent physiology.

The winter annual *B. tectorum* is known to have a higher growth rate than native perennial grasses (e.g., *Pseudoroegneria spicata* (Pursh) A. Löve and populations of *Elymus elymoides* (Raf.) Swezey [21]), particularly at low temperature [22–24]. A comparison of calorimetrically measured growth rates of *B. tectorum* (Fig. 4) and *P. secunda* (Figs. 3a–3c) confirm this difference at lower temperature (i.e., 10°C). Growth rates and metabolic efficiency for all *B. tectorum* populations were relatively greater than those of *P. secunda* at 10°C. Consequently, both species maintain positive growth and efficiency at low temperatures, but rates for *B. tectorum* are relatively greater than *P. secunda*. Lower growth rate in *P. secunda* at low temperature may translate into less ability to compete with *B. tectorum* for soil moisture when it is temporarily plentiful in early spring. *B. tectorum* may thus experience less water stress than *P. secunda* as soil water diminishes in summer (e.g., [4]).

Greater growth and efficiency at high temperature (20°C) in *P. secunda* compared to *B. tectorum* may be a mechanism that partially facilitates *P. secunda* persistence during the dry season. Unlike *B. tectorum*, metabolic efficiency and growth rate of *P. secunda* populations generally remained positive over the temperature range of 10 to 20°C. In addition, metabolic efficiency of many *P. secunda* populations sharply increased with temperature in late season when available soil moisture and growth are most limiting. Although we did not measure soil moisture depletion at the research sites, the gradual decreases in q and R_{CO_2} were greater for the more xeric garden (Orchard), suggesting that plant growth and senescence were partially induced by water stress.

Our laboratory experiment indicated a relatively small amount of variation in R_{CO_2} and Q_{10} values among populations within the range of 10 to 30°C. In addition, our calorimetry data demonstrate that *P. secunda* and *B. tectorum* primarily differ in temperature-dependent physiology at high temperature. In spite of this key difference, these species have similar phenological development characterized by early spring growth and rapid senescence with soil moisture depletion. However, the annual *B. tectorum* dies, and the perennial *P. secunda* survives the dry period. Future research may unveil additional mechanisms associated with the ability of *P. secunda* to persist. We suggest that a positive growth rate and greater metabolic efficiency at high temperature of *P. secunda* than *B. tectorum* may be associated with the persistence of *P. secunda* during the dry season.

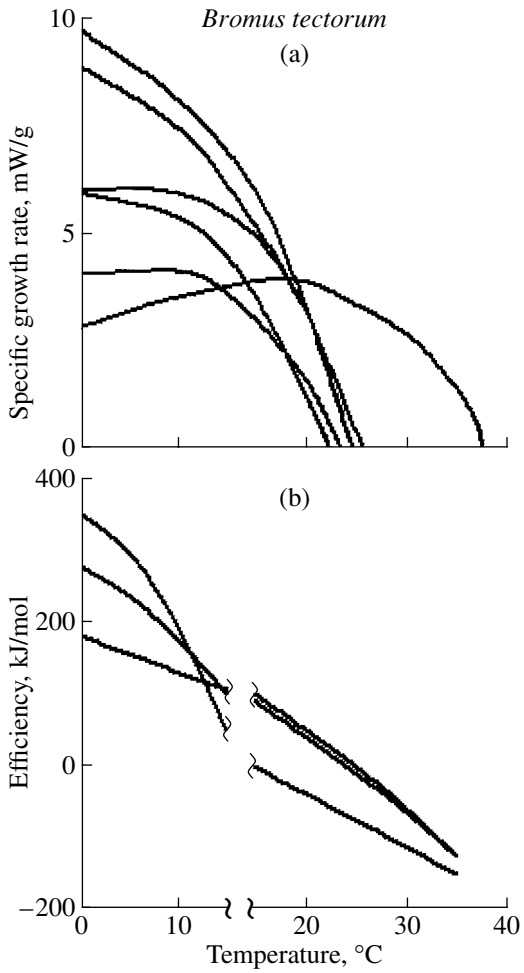

Fig. 4. (a) Specific growth rates ($R_{SG}\Delta H_B$) and (b) efficiency of converting photosynthetic substrate to structural carbon ($[\varepsilon/(1-\varepsilon)]\Delta H_B$) of three to six *B. tectorum* populations measured as a function of temperature. Figure is redrawn after Hemming *et al.* [12].

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REFERENCES

1. Pickford, G.D., The Influence of Continued Heavy Grazing and of Promiscuous Burning on Spring–Fall Ranges in Utah, *Ecology*, 1932, vol. 13, pp. 159–171.
2. Mack, R.N., Invasion of *Bromus tectorum* L. into Western North America: An Ecological Chronicle, *Agro-Ecosystems*, 1981, vol. 7, pp. 145–165.
3. Billings, W.D., *Bromus tectorum*, a Biotic Cause of Ecosystem Impoverishment in the Great Basin, *The Earth in Transition: Patterns and Processes of Biological Impoverishment*, Woodell, G.M., Ed., Cambridge: Cambridge Univ. Press, 1990, pp. 301–322.
4. Link, S.O., Gee, G.W., and Downs, J.L., The Effect of Water Stress on Phenological and Ecophysiological Characteristics of Cheatgrass and Sandberg's Bluegrass, *J. Range Management*, 1990, vol. 43, pp. 506–513.
5. Wright, H.A. and Klemmenson, J.O., Effects of Fire on Bunchgrass of the Sagebrush–Grass Region in Southern Idaho, *Ecology*, 1965, vol. 46, pp. 680–688.
6. Daubenmire, R., *Steppe Vegetation of Washington*, Washington Agricultural Experiment Station Technical Bulletin, 1970.
7. Rickard, W.H., Vegetation of Knob and Kettle Topography in South–Central Washington, *Northwest Sci.,* 1975, vol. 49, pp. 147–152.
8. Daubenmire, R., Annual Cycles of Soil Moisture and Temperature as Related to Grass Development in the Steppe of Eastern Washington, *Ecology*, 1972, vol. 53, pp. 419–424.
9. Hansen, L.D., Hopkin, M.S., Rank, D.R., Anekonda, T.S., Breidenbach, R.W., and Criddle, R.S., The Relation between Plant Growth and Respiration: A Thermodynamic Model, *Planta*, 1994, vol. 194, pp. 77–85.
10. Hansen, L.D., Taylor, D.K., Smith, B.N., and Criddle, R.S., The Relation between Plant Growth and Respiration: Applications to Ecology and Crop Cultivar Selection, *Russ. J. Plant Physiol.*, 1996, vol. 43, pp. 691–697.
11. Criddle, R.S. and Hansen, L.D., Calorimetric Methods for Analysis of Plant Metabolism, *Handbook of Thermal Analysis and Calorimetry*, Kemp, R.B., Ed., Amsterdam: Elsevier, 1999, vol. 4, pp. 711–763.
12. Hemming, D.J.B., Meyer, S.E., Smith, B.N., and Hansen, L.D., Respiration Characteristics Differ among Cheatgrass (*Bromus tectorum* L.) Populations, *Great Basin Naturalist*, 1999, vol. 59, pp. 355–360.
13. McCarlie, V.W., Hansen, L.D., Smith, B.N., Monsen, S.B., and Ellingson, D.J., Anabolic Rates Measured with Calorespirometry for Eleven Subpopulation of *Bromus tectorum* Match Temperature Profiles of Local Microclimates, *Russ. J. Plant Physiol.*, 2003, vol. 50, pp. 183–191.
14. USDA, *Soil Survey. Ada County Area, Idaho*, Washington: US Department of Agriculture, Soil Conservation Service, 1980.
15. USDA, *Soil Survey. Fairfield-Nephi Area, Utah*, Washington: US Department of Agriculture, Soil Conservation Service, 1984.
16. SAS Institute Incorporate, *SAS/STAT Users Guide, Release 6.03*, Cary: SAS Institute Inc., 1989.
17. Criddle, R.S., Smith, B.N., and Hansen, L.D., A Respiration Based Description of Plant Growth Rate Responses to Temperature, *Planta*, 1997, vol. 201, pp. 441–445.
18. Ott, R.L., *An Introduction to Statistical Methods and Analysis*, Belmont: Wadsworth, Inc., 1993.
19. Morrow, L.A. and Stahlman, P.W., The History and Distribution of Downy Brome (*Bromus tectorum*) in North America, *Weed Sci.,* 1984, vol. 32, suppl. 1, pp. 2–6.
20. Knapp, P.A., Cheatgrass (*Bromus tectorum* L.) Dominance in the Great Basin Desert, *Global Environ. Change*, 1996, vol. 6, pp. 37–52.
21. Arredondo, J.T., Jones, T.A., and Johnson, D.A., Seedling Growth of Intermountain Perennial and Weedy Annual Grasses, *J. Range Management*, 1998, vol. 51, pp. 584–589.
22. Hulbert, L.C., Ecological Studies of *Bromus tectorum* and Other Annual Bromegrasses, *Ecol. Monogr.*, 1955, vol. 25, pp. 181–213.
23. Harris, G.A., Some Competitive Relationships between *Agropyron spicatum* and *Bromus tectorum, Ecol. Monogr.*, 1967, vol. 37, pp. 89–111.
24. Aguirre, L. and Johnson, D.A., Influence of Temperature and Cheatgrass Competition on Seedling Development of Two Bunchgrasses, *J. Range Management*, 1991, vol. 44, pp. 247–354.